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HAMULONEMA GEN. NOV. FOR TELADORSAGIA HAMATA AND OSTERTAGIA KENYENSIS IN THE OSTERTAGIINE FAUNA (NEMATODA: TRICHOSTRONGYLOIDEA) FROM AFRICAN UNGULATES

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ABSTRACT: *Hamulonema* gen. nov. is proposed for *Teladorsagia hamata* and *Ostertagia kenyensis* in the ostertagiine nematode fauna found in artiodactyl hosts from Africa. Monomorphic species representing this genus are characterized by a bilaterally symmetrical and parallel synlophes in males and females, a 2-2-1 bursal formula, an accessory bursal membrane that is strongly cuticularized and reduced, a strongly reduced dorsal lobe and ray, and robust spicules with a simple, weakly pointed, ventral process, and curved, hooklike dorsal process. Species referred to *Hamulonema* nov. gen. are immediately distinguished from those of *Camelostrongylus*, *Longistrongylus*, *Marshallagia*, *Orloffia*, *Ostertagia*, and *Pseudommarshallagia* in which the bursal formula is 2-1-2 in males. *Hamulonema* nov. gen. is distinguished from those genera having a 2-2-1 bursa, including *Africanaststrongylus*, *Cervicaprastrongylus*, *Hyostrongylus*, *Mazamastrongylus*, *Sarwaria*, *Spiculoptera*, and *Teladorsagia* by the structure of the synlophes, bursa, genital cone, “0” and “7” papillae, dorsal lobe, and spicules in specific instances. In the global fauna, 4 of 14 ostertagiine genera are endemic to Africa. African genera may represent morphologically divergent and discrete or historically isolated lineages reflecting a pattern of geographic and host colonization as a driver for diversification since the Miocene.

Abomasal nematodes (Ostertagiinae: Trichostrongyloidea) currently include 13 genera in the global fauna (Hoberg and Abrams, 2007; Hoberg et al., 2008). Morphologically, 2 distinct groups are recognized based on the structure and relative positions of rays that support the copulatory bursa of males (Gibbons and Khalil, 1982a; Durette-Desset, 1983; Jansen, 1989; Hoberg and Lichtenfels, 1994; Durette-Desset et al., 1999). Among ostertagiines, species of 6 genera are characterized by a 2-1-2 bursal formula, i.e., *Camelostrongylus* Orloff, 1933, *Longistrongylus* LeRoux, 1931, *Marshallagia* (Orloff, 1933), *Orloffia* Drózdź, 1965, *Ostertagia* Ransom, 1907, and *Pseudommarshallagia* (Roetti, 1941). Alternatively, a 2-2-1 pattern is typical among species of 7 genera, i.e., *Africanaststrongylus* Hoberg, Abrams, and Ezenwa, 2008, *Cervicaprastrongylus* Gibbons and Khalil, 1982, *Hyostrongylus* Hall, 1921, *Mazamastrongylus* Cameron, 1935, *Sarwaria* Drózdź, 1965, *Spiculoptera* (Orloff, 1933), and *Teladorsagia* Andreeva and Satubaldin, 1954.

Among the fauna of medium stomach worms referred to the Ostertagiinae endemic to Africa, 2 species are regarded as having uncertain affinities. The problematic nature of generic-level identity for *Teladorsagia hamata* (Mönnig, 1932) and *Ostertagia kenyensis* Gibbons and Khalil, 1982, was highlighted during studies that established *Africanaststrongylus* among artiodactyl hosts (Hoberg et al., 2008). Gibbons and Khalil (1980) recognized the structural similarity of these nematodes, both with a 2-2-1 bursal formula, and distinguished specimens of *O. kenyensis* from those of *T. hamata* based in part on the configuration of the dorsal process of the spicules, which were considered to lack a prominent hooklike structure in the former species. *Ostertagia kenyensis* was originally described based on specimens in Damara Dik Dik (*Madaqua kirkii* Günther) and Grant's gazelle (*Gazella granti* Brooke) from Kenya (Gibbons and Khalil, 1980), but has not been found subsequently (Hoberg et al., 2008). *Teladorsagia hamata* was based on specimens in springbok (*Antidorcas marsupialis* Zimmerman) and was later

found in Bontebok (*Damaliscus pygargus* Pallas) from South Africa (Mönnig, 1932; Hoberg et al., 2008). The latter nematode species, originally described in *Ostertagia* Ransom, 1907, was later transferred to *Spiculoptera* by Travassos (1937), to *Aptera* Jansen, 1958 by Jansen (1958), and most recently to *Teladorsagia* by Durette-Desset (1989).

In establishing *Africanaststrongylus*, we identified structural inconsistencies for placement of either *T. hamata* or *O. kenyensis* among any known genera of the Ostertagiinae, noted details concerning morphology, and outlined a preliminary proposal to designate a new genus for these species (Hoberg et al., 2008). Meristic data and general comparisons for these species, particularly with respect to comparisons with *Africanaststrongylus buceros* Hoberg, Abrams and Ezenwa, 2008 have been presented previously (Hoberg et al., 2008). In the context of the current study, we now expand on our proposal to resolve generic-level taxonomy for these species and provide comparative morphological criteria for the diagnosis of a new genus in the subfamily.

MATERIALS AND METHODS

Specimens examined

Specimens of *T. hamata* and *O. kenyensis* included material from the original type series for both species. Representatives of all genera characterized by a 2-2-1 bursal formula were available for study and examined, except specimens of *Cervicaprastrongylus*. In the case of the latter genus, detailed descriptions and re-descriptions serve as the basis for comparison (e.g., Durette-Desset and Chabaud, 1974; Durette-Desset and Denke, 1978; Gibbons and Khalil, 1982b). Specimens representing all genera endemic to Africa were examined, except *Pseudommarshallagia elongata* (Roetti, 1941). Specimens and sources for species of ostertagiine nematodes used in comparative morphological studies are listed in Table I.

Microscopy

Nematodes were prepared as temporary whole mounts cleared in phenol-alcohol (80 parts melted phenol crystals and 20 parts absolute ethanol) and examined with interference contrast microscopy. The synlophes was studied in whole mounts with particular attention to the pattern of ridge systems in the cervical zone (Lichtenfels et al., 1988).

Male specimens were evaluated on the basis of the copulatory bursa, genital cone, and spicules. Bursal ray patterns were determined and

TABLE I. Specimens of *Hamulonema* gen. nov. and other ostertagiines examined.

Accession*	Species (original identification)	Host	Locality	♂†	♀†
<i>Hamulonema</i> gen. nov.					
OHC 2366‡§	<i>Teladorsagia hamata</i>	<i>Antidorcas marsupialis</i>	South Africa	Not available	
UP T-2053	<i>T. hamata</i>	<i>A. marsupialis</i>	South Africa	1	—
BNH 1998.10.26.22–26§	<i>Ostertagia kenyensis</i>	<i>Gazella granti</i>	Kenya	2	2
		<i>Madoqua kirkii</i>	Kenya		
Other genera and species of ostertagiines					
USNPC 66322.02, 86939, 99545, 99546, 99551‡§	<i>Africanastrongylus buceros</i>	<i>Syncerus caffer</i>	Uganda	13	12
USNPC 99547§	<i>A. buceros</i>	<i>S. caffer</i>	Kenya	—	5
USNPC 99548, 99549§	<i>A. buceros</i>	<i>S. caffer</i>	South Africa	2	3
USNPC 82538#	<i>Hyostongylus rubidus</i>	<i>Sus scrofa</i>	Washington, D.C.	2	2
USNPC 81213	<i>Longistongylus curvispiculum</i> ¶	<i>Ovis aries</i>	Texas	2	—
USNPC 77484	<i>Longistongylus sabie</i> **	<i>Aepyceros melampus</i>	South Africa	4	—
USNPC 66325	<i>Longistongylus schrenki</i> ††	<i>Ourebia ourebi</i>	Uganda	4	—
USNPC 66323	<i>L. schrenki</i>	<i>Kobus kob</i>	Uganda	2	—
KISIH 19140	<i>Mazamastrongylus dagestanica</i> ‡‡	<i>Alces alces</i>	Russia	2	—
USNPC 74139	<i>Sarwaria bubalis</i> §§	<i>Bos taurus</i>	Guyana	2	—
USNPC 82742	<i>Spiculopteria spiculoptera</i>	<i>Cervus elaphus</i>	Texas	2	—
USNPC 87905.01, 87905.02§	<i>Teladorsagia boreoarcticus</i> ##	<i>Ovibos moschatus</i>	Northwest Territory, Canada	4	4

* Collection numbers from the U.S. National Parasite Collection (USNPC), Onderstepoort Helminthological Collection (OHC), the Natural History Museum, London (BNH), University of Pretoria (UP), and the K.I. Skrjabin Institute of Helminthology, Moscow (KISIH).

† Number of male and female specimens examined.

‡ Including holotype male and allotype female.

§ Including paratypes.

¶ Syntype, from original collection by H. O. Mönnig, on 1 August 1931 at Houtkraal Farm, Karoo, Cape Province, derived from host following transport to Pretoria Zoo (Mönnig, 1932).

Lectotype and paralectotype specimens (see Hoberg et al., 1993b).¶ *Longistongylus curvispiculum* represents a species previously referred to *Bigalkenema*; material examined represents an introduced population in western Texas and was from an experimental infection in domestic sheep based on larvae recovered from *Oryx biesa* (data from Craig, 1993).

** *Longistongylus sabie* represents a species previously referred to *Bigalkenema*.

†† *Longistongylus schrenki* represents the species previously referred to *Kobusinema*.

‡‡ Details for *M. dagestanica* are in Hoberg and Khurstalev (1996).

§§ Details for *Sarwaria* are in Lichtenfels et al. (1996).

||| Details for *S. spiculoptera* are in Rickard et al. (1993).

Details for *T. boreoarcticus* are in Hoberg et al. (1999).

described using the system of Durette-Desset and Chabaud (1981) and Durette-Desset (1983). Papillae of the genital cone and rays of the bursa followed the numbering system of Chabaud et al. (1970). The structure of the ovejectors was evaluated in the context of recent definitions and descriptions among related nematodes (Lichtenfels et al., 2003).

Host nomenclature

Taxonomy for hosts follows Wilson and Reeder (1993) in the text and Table I. Host listings have been modified from those reported in the original literature to reflect current usage and understanding of ungulate taxonomy.

RESULTS

Observations on morphology in *O. kenyensis* and *T. hamata*

Paratype specimens of *O. kenyensis* and a syntype specimen of *T. hamata* were in general agreement with original descriptions (Mönnig, 1932; Gibbons and Khalil, 1980; Hoberg et al., 2008). We comment below on observations from specimens of both species for characters not considered in the original descriptions (Figs. 1–26). Based on the comparative morphological observations presented below and details of the original descriptions and comparisons among genera of the Ostertagiinae (Hoberg et al., 2008), we conclude that *O. kenyensis* and

T. hamata are morphologically similar congeners representing an undetermined genus.

Esophageal and cervical structures

A prominent valve (EIV) is present at the esophageal–intestinal junction (Figs. 1, 11). The EIV is cylindrical and not laterally inflated. The excretory pore, orifices of the subventral esophageal glands, and cervical papillae are near the same level in the cervical region.

Synlophe

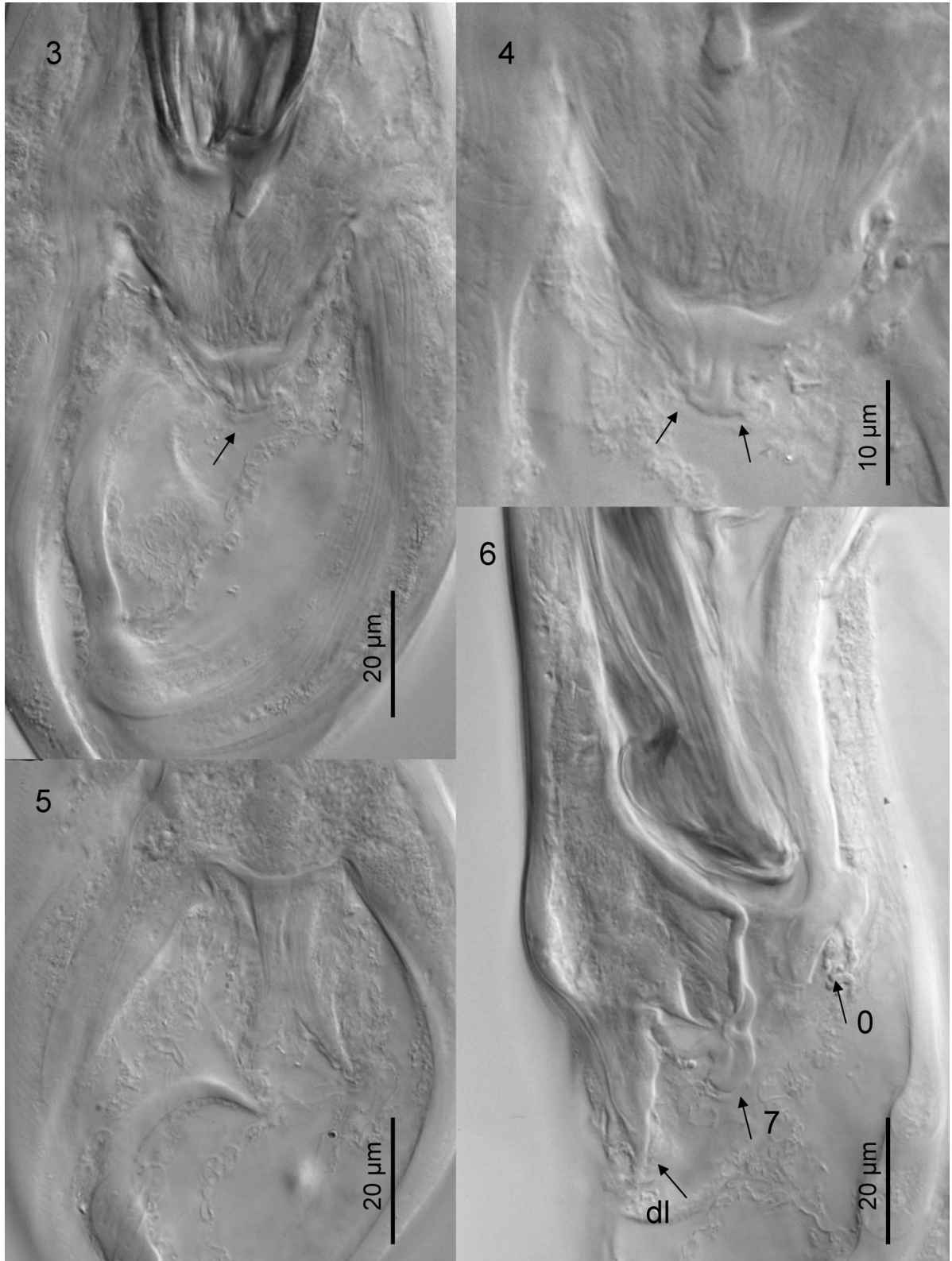
The synlophe is well developed, symmetrical, perpendicular in orientation, and lacking in gradient. In the cervical region, lateral ridges are disposed in a parallel, Type 2, pattern (Fig. 12). Ridges extend to near the caudal extremity in males and females. Overall the cervical pattern is similar between *O. kenyensis* and *T. hamata*, but the specific numbers of ridges vary (Mönnig, 1932; Gibbons and Khalil, 1980).

Bursal structure and genital cone

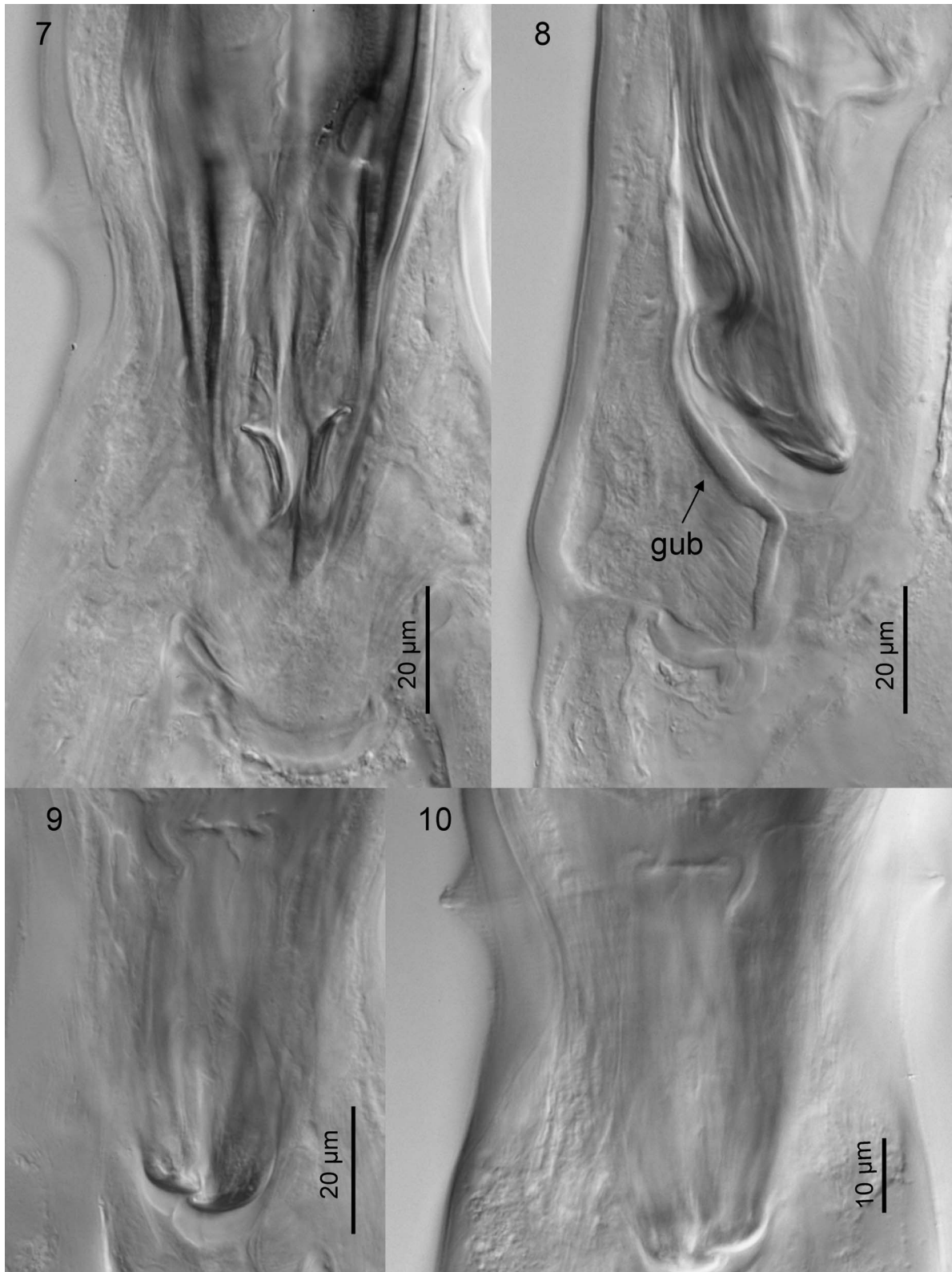
The bursa is symmetrical and bilobed, prebursal papillae are prominent, and a proconus is absent in males of both species



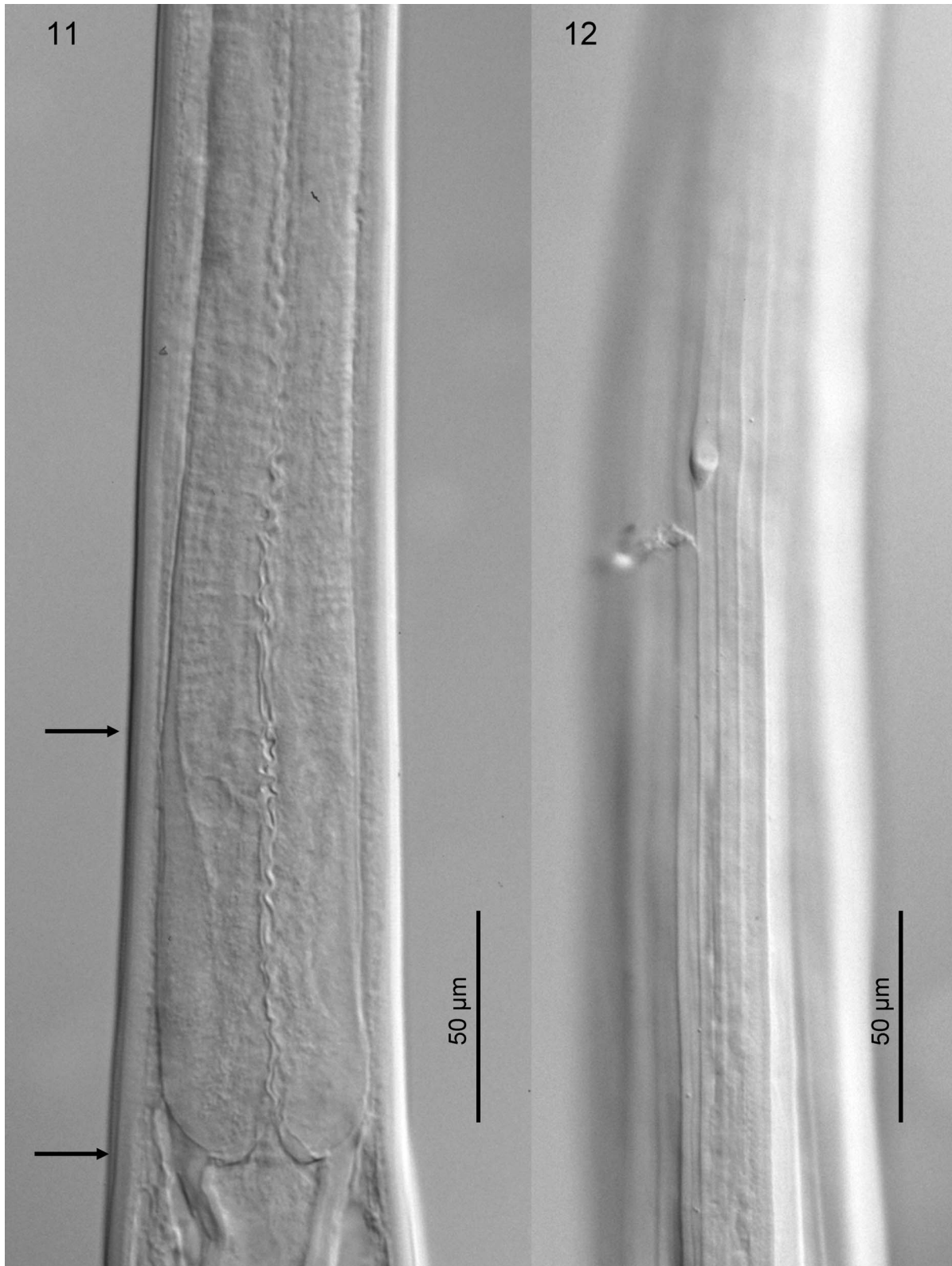
FIGURES 1 and 2. *Hamulonema hamata* gen. nov., nov. comb., showing esophageal and bursal structure in syntype male specimen. (1) Basal region of esophagus in lateral view, showing structure of esophageal-intestinal valve (between arrows). (2) Copulatory bursa in ventral view, showing position of prominent prebursal papillae (pbp), accessory bursal membrane (abm), and robust spicules with trifurcation near 60% (arrow).



FIGURES 3–6. *Hamulonema hamata* gen. nov., nov. comb., showing structure of genital cone and dorsal lobe in syntype male specimen. (3) Cuticularized and reduced accessory bursal membrane in dorsal view, showing relative position in the genital cone (arrow). (4) Accessory bursal membrane in ventral view, showing platelike structure, thickened cuticularized margin distally, and parallel “7” papillae terminating along distal edge (arrows). (5) Dorsal ray in ventral view showing stout base with parallel margins, and primary bifurcation. (6) Genital cone in right lateral view, showing relative positions of the dorsal lobe (dl), “7” papillae contained in the relatively solid accessory bursal membrane (7), and acutely pointed “0” papillae (0).



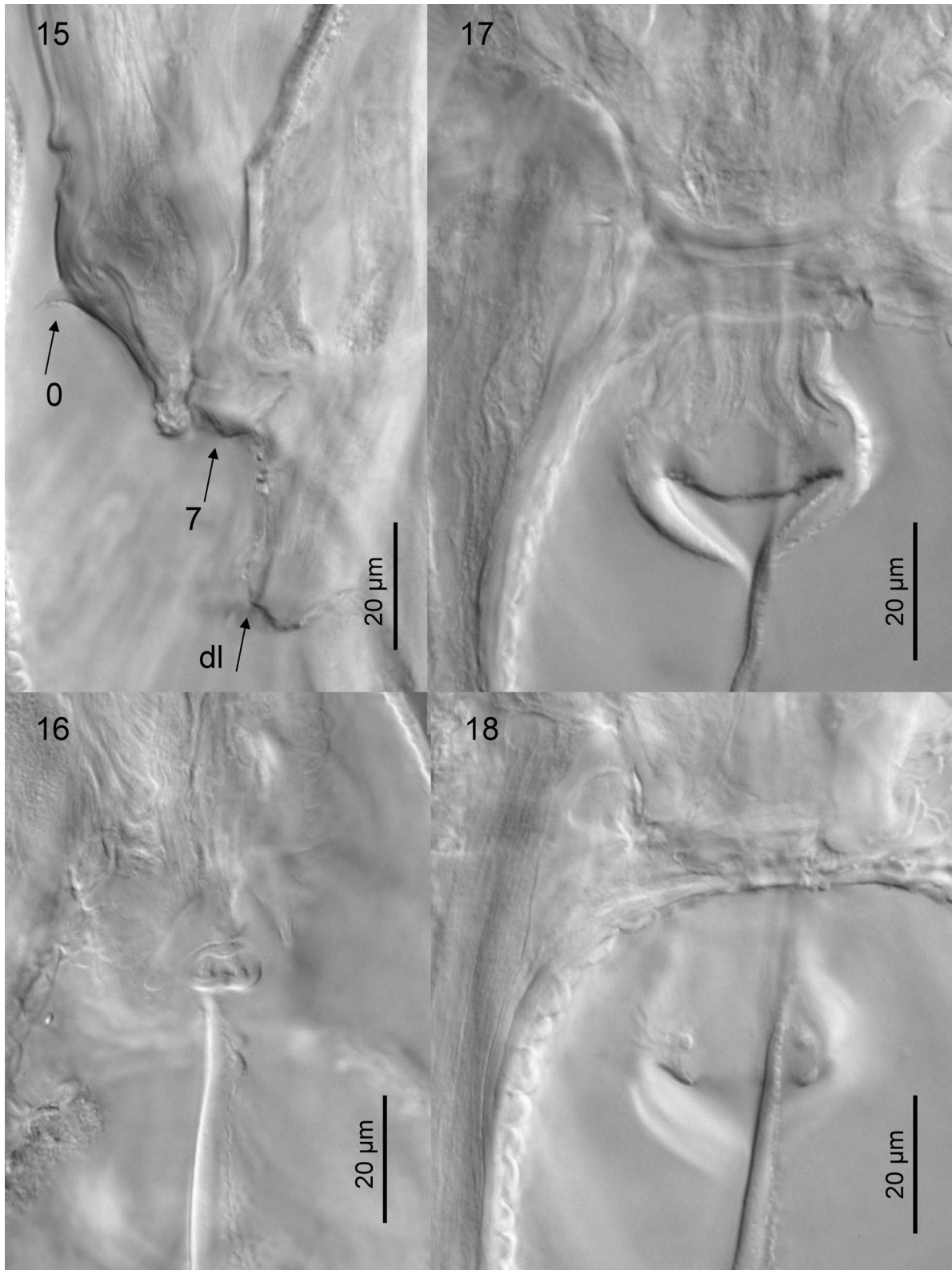
FIGURES 7–10. *Hamulonema hamata* gen. nov., nov. comb., showing structure of spicules and gubernaculum in syntype male specimen. (7) Spicule tips in dorsal view, showing arcuate or curved hooklike termination of dorsal processes. (8) Spicule tips and gubernaculum (gub) in right lateral view. Note structure of sinuous and narrow gubernaculum, ventrally curved dorsal process, and bluntly pointed termination of main shaft. (9) Spicule tips in ventral view, showing hyaline sheath and medially directed termination of main shafts. (10) Prebursal papilla in dorsal view.



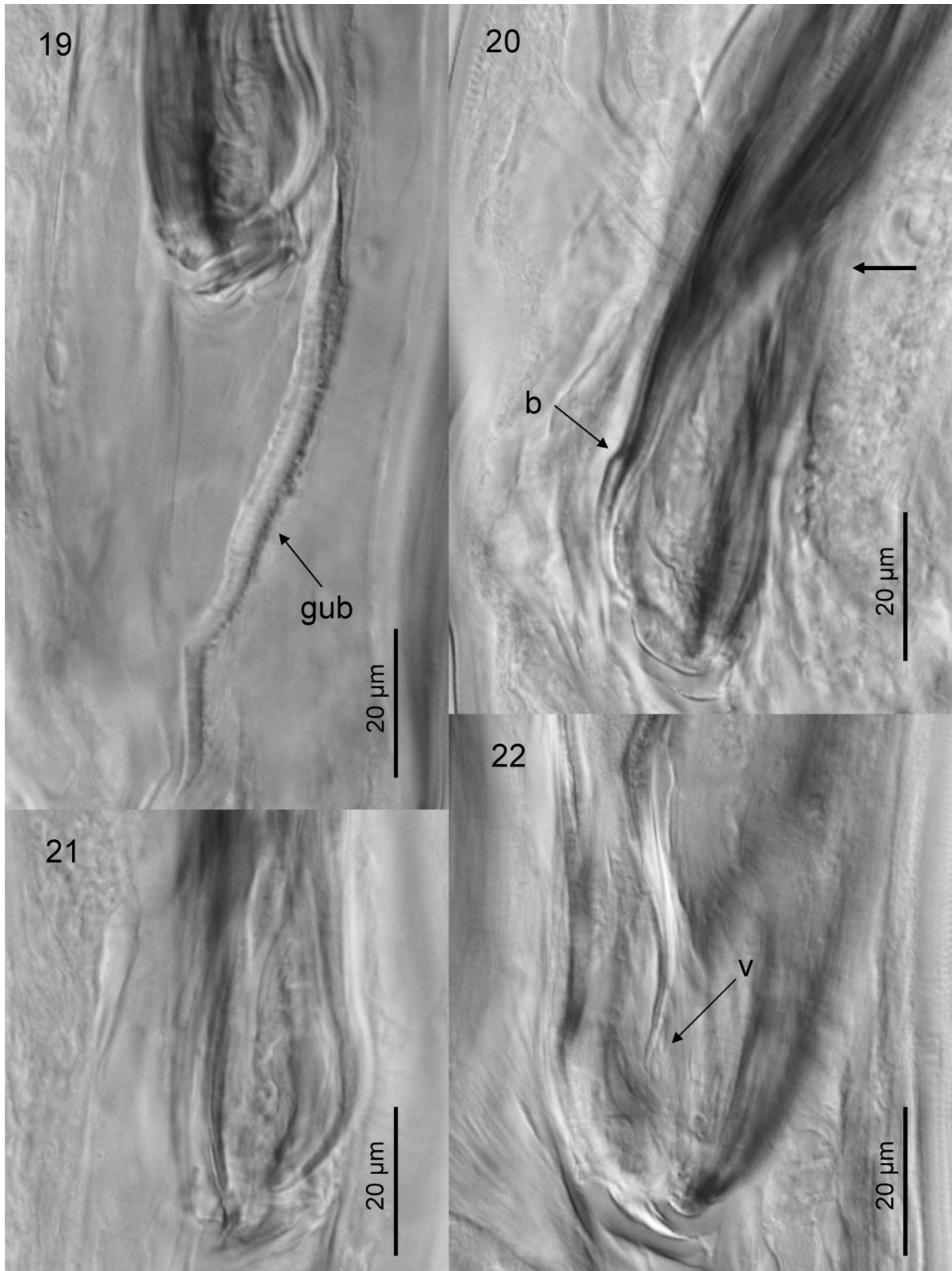
FIGURES 11 and 12. *Hamulonema kenyensis* gen. nov., nov. comb., showing esophageal and cervical structure in a female paratype specimen. (11) Structure of basal esophagus and esophageal-intestinal valve (between arrows) in lateral view. (12) Cervical synlophe in lateral view, showing parallel or Type 2 system and prominent, thornlike cervical papilla.



FIGURES 13 and 14. *Hamulonema kenyensis* gen. nov., nov. comb., showing structure of bursa in a male paratype specimen. (13) Copulatory bursa in dorsal view, showing prominent but reduced dorsal lobe, relative position of trifurcation in robust spicules (arrow), and medially directed main processes with hyaline sheath. (14) Copulatory bursa in left lateral view, showing general form, relative positions of spicules with trifurcation near 60% (arrow), gubernaculum (gub), "0" papillae (0), reduced accessory bursal membrane (7), and dorsal lobe (dl).



FIGURES 15–18. *Hamulonema kenyensis* gen. nov., nov. comb., showing structure of genital cone and dorsal lobe in a male paratype specimen. (15) Genital cone in left lateral view, showing “0” papillae in protruding membrane (0), reduced accessory bursal membrane with “7” papillae (7), and rounded dorsal lobe (dl). (16) Structure of “0” papillae contained in membrane, ventral view. (17) Dorsal ray in ventral view showing stout base with parallel margins, and primary bifurcation. (18) Dorsal ray in ventral view, showing positions of lateroventrally directed papillae, Rays 9/10.



FIGURES 19–22. *Hamulonema kenyensis* gen. nov., nov. comb., showing structure of spicules and gubernaculum in a male paratype specimen. (19) Gubernaculum (gub) and spicules in left lateral view, showing relative positions and form; note ventrally curved dorsal process of spicule tip. (20) Spicule tip in right lateral view, showing point of trifurcation (arrow) and curved dorsal process with miniscule barb (b). (21) Spicule tip in left lateral view, showing curved dorsal process. (22) Spicule tip, in medial view, showing narrow ventral process lacking ornamentation (v).



FIGURES 23–26. *Hamulonema kenyensis* gen. nov., nov. comb., showing structure of ovejectors and tail in female paratype specimen. (23) Ovejector in right lateral view, showing posterior region from level of vestibule (ve) to termination of posterior infundibulum (inf, between dotted arrows). Note structure of sphincter (sp, between heavy black arrows) with bulblike sphincter-1 (s1) and elongate sphincter-2 (s2) and the position of the vulva (vu). (24) Vulva in lateral view. (25) Tail, ventral view. (26) Tail, right lateral view, showing position of anus.

(Figs. 2, 6, 10, 13–15). Bursal bosses are typical in *O. kenyensis*, but absent in *T. hamata*. The bursal ray formula is 2-2-1. Rays 2/3 are divergent through their length, and convergent distally; Rays 2 are less massive relative to Rays 3. Rays 4/5 are equal in length, parallel, straight, and relatively narrow, extending to near the margin of the bursal membrane where the tips are slightly divergent. Rays 6 are narrow and elongate, curving medially and terminating at the bursal margin. Rays 8 are stout (Fig. 5), of near-constant diameter through their length, and curved medially. The dorsal lobe is strongly reduced, and curves ventrally relative to Rays 8 in lateral view (Figs. 5, 6, 15, 17, 18). Rays 9/10 are relatively robust basally, but not strongly inflated, and are $\leq 50\%$ of the length of the externodorsal rays. The dorsal ray has a primary bifurcation near 66–69% in the distal third from the anterior; primary branches of the dorsal ray terminate in bifurcate papillae of Rays 9/10, which are directed ventrolaterally (Figs. 5, 17, 18).

In both species, the miniscule, divergent, and acutely pointed “0” papillae are located on the ventral aspect of the genital cone. In *O. kenyensis*, the papillae are enveloped in a conspicuous rounded membrane, which protrudes ventrally (Figs. 15, 16).

The accessory bursal membrane is reduced, inconspicuous, and strongly cuticularized. In *T. hamata*, the “7” papillae are parallel and contained within a platelike structure extending posteriorly from the dorsal aspect of the genital cone (Figs. 3, 4, 6). In *O. kenyensis*, the reduced accessory bursal membrane could not be discerned clearly in the specimens available.

Spicule and gubernaculum structure

The alate spicules are robust and straight in lateral and ventral view, with a trifurcation near 60% from the capitulum and a prominent ostertagiine window (Figs. 2, 7–9, 13, 19–22). The main shaft terminates in a hyaline membrane, and the tips turn mediad. The ventral process is narrow, bluntly pointed, and lacking in ornamentation. The dorsal process is approximately twice the length of the ventral process, and adorned with a curved hooklike terminal region demarcated anteriorly by a barb. In *T. hamata*, the distal hook is prominent (Figs. 7, 8), whereas in *O. kenyensis* it is weakly developed, curved, and not visible in all orientations (Figs. 19, 20). Spicule structure is an unequivocal character that differentiates these species. The gubernaculum is elongate and narrow in dorsoventral view; in lateral view, it appears sinuous (Figs. 8, 14, 19)

Ovejectors and female tail

The ovejectors are typical of ostertagiine nematodes (Lichtenfels et al. 2003). In specimens of *O. kenyensis*, there are paired infundibula, bipartite sphincters composed of a bulbous and cylindrical component, and a vestibule that is confluent with the vulva (Figs. 23, 24). The tail is simple, and without marked annulations near the caudal extremity (Figs. 25, 26).

MORPHOLOGICAL DIAGNOSIS

Hamulonema gen. nov.

Diagnosis: Trichostrongylidae. Small uncoiled nematodes with well developed bilateral parallel synlophe, prominent thornlike cervical papillae and esophageal–intestinal valve in

males and females. Males monomorphic. Bursal structure 2-2-1, symmetrical; discrete fields of bosses present or absent. Rays 2/3 divergent through length, convergent distally. Rays 4/5 equal in length, parallel, relatively straight, narrow, minimally divergent at tips. Accessory bursal membrane and “7” papillae reduced, complex, strongly cuticularized. Rays 8 robust, curved mediad. Dorsal lobe strongly reduced, curving ventrally relative to Rays 8; dorsal ray, or Rays 9/10, with stout base parallel throughout length, bifurcate in distal third. Spicules robust, trifurcate, with simple weakly pointed ventral process, and curved, hooklike dorsal process. Females amphidelphic with transverse vulva in posterior quarter; cuticular inflations at level of vulva may be present.

Taxonomic summary

Type species: *Hamulonema hamata* (Mönnig, 1932) gen. nov., nov. comb., in springbok, *A. marsupialis* (Zimmerman) and Bontebok, *D. pygargus* (Pallas) from South Africa. Syntype male from original collection by Mönnig (1932); syntype series at University of Pretoria under UP-T 2053 with single male specimen now held in the U.S. National Parasite Collection as USNPC No. 100216.

Other species: *Hamulonema kenyensis* (Gibbons and Khalil, 1980) gen. nov., nov. comb. in Damara Dik Dik, *M. kirkii* (Günther) and Grant’s gazelle, *G. granti* Brooke from Kenya.

Etymology: *Hamulonema* is derived from the Latin diminutive *hamulus* and Greek *nema* denoting the hooklike dorsal process of the spicules characteristic of these nematodes.

DISCUSSION

Establishing *Hamulonema* gen. nov.

Currently, 13 genera, diagnosed morphologically by a suite of putative synapomorphies for the subfamily, are represented among the Ostertagiinae (Hoberg and Abrams, 2007; Hoberg et al., 2008). The problematic nature and incompatibility for the current taxonomy of *O. kenyensis* in *Ostertagia* and *T. hamata* in *Teladorsagia* has been recognized. Neither species appears morphologically consistent with any known genus attributed to the subfamily. Among the group of 7 genera having a 2-2-1 bursa and either a tapering or a parallel lateral synlophe, a suite of structural characters would negate an unequivocal diagnosis for either species.

Species referred to *Hamulonema* nov. gen., including the designated type *H. hamata* nov. comb. and congeneric *H. kenyensis* nov. comb., are immediately distinguished from species of *Camelostrongylus*, *Longistrongylus*, *Marshallagia*, *Orloffia*, *Ostertagia*, and *Pseudommarshallagia* by the structure of the 2-2-1 bursa in males (Durette-Desset, 1983; Hoberg et al., 2008). Although a suite of additional structural characters further distinguishes *Hamulonema* from all species referred to these genera, this fundamental difference in the configuration of the bursa is sufficient as a primary diagnostic attribute (Durette-Desset, 1983; Hoberg and Lichtenfels, 1994; Durette-Desset et al., 1999).

In contrast, among ostertagiines with a 2-2-1 bursa, *Hamulonema* can be distinguished in the following manner. In *Spiculopteragia* and *Mazamastrongylus* the presence of a unique “hood-ridge” system in the ventral cervical synlophe, a strong-

ly tapering lateral synlophe, a liplike and protruding excretory pore, a bursa with Rays 4 <5 in length, robust Rays 4, and membranous accessory bursal membrane with divergent and filamentous “7” papillae (or prominent Sjöberg’s organ in minor morphotypes) differentiate these genera from *Hamulonema* (Andreeva, 1958; Lichtenfels et al., 1993; Drózdź, 1995; Hoberg, 1996; Hoberg and Khurstalev, 1996). Further, among species of *Spiculopteragia*, males are polymorphic and spicules are adorned with prominent fanlike membranes (Drózdź, 1995); the dorsal process of the spicules among species of *Mazamastrongylus* is consistently spoonlike (Hoberg, 1996).

A parallel, Type 2 cervical synlophe and other attributes serve to differentiate *Hamulonema* from *Teladorsagia*, *Sarwaria*, and *Africanastrongylus*. In *Teladorsagia*, polymorphism among males, a tapering cervical synlophe, robust Rays 4, an elongate dorsal ray and lobe that are not disposed ventrally to the elongate, and straight Rays 8 represent consistent differences relative to species of *Hamulonema* (Andreeva, 1956, 1958; Drózdź, 1965, 1995; Hoberg et al., 1999). *Hamulonema* is also clearly distinguished from *Sarwaria* and *Africanastrongylus*, which contain species with a tapering, Type 1, lateral synlophe, miniscule, but thornlike, cervical papillae, and a reduced but laterally inflated dorsal lobe, disposed ventrally (Lichtenfels et al., 1996; Hoberg and Abrams, 2007; Hoberg et al., 2008). *Sarwaria*, including *S. bubalis* (Sarwar, 1956) and *S. caballeroi* (Chabaud, 1977), contrasts with *Hamulonema* in having Rays 2/3 weakly divergent along their entire length, Rays 4 <5 in length, robust Rays 4, relatively narrow Rays 8, an accessory bursal membrane with narrow filamentous “7” papillae, and absence of a gubernaculum (Drózdź, 1965; Chabaud, 1977; Lichtenfels et al., 1996; Hoberg and Abrams, 2007). In *Africanastrongylus*, presence of a proconus, a well-developed bilobed accessory bursal membrane containing divergent and filamentous “7” papillae, massive Rays 8 and Rays 9/10 (in *H. kenyensis* and *H. hamata* these rays have bases that are not strongly inflated), an alate gubernaculum, and filamentous spicules that trifurcate near 80% from the anterior constitute diagnostic characters relative to *Hamulonema* (Hoberg et al., 2008).

Hamulonema is most similar to *Cervicaprastrongylus* and *Hyostrongylus* in the structure of the parallel cervical synlophe (Type 2 lateral), absence of a proconus, presence of a reduced accessory bursal membrane, and a bursa in which Rays 4/5 are parallel and not strongly divergent distally. *Hamulonema* is distinguished from these genera by a markedly reduced dorsal lobe and ray disposed ventrally, a consistently different pattern of bifurcation for Rays 9/10, reduced and robust Rays 8, and acutely pointed, divergent “0” papillae (Gibbons and Khalil, 1982a, 1982b; Durette-Desset et al., 1992; Hoberg et al., 1993b). In species belonging to *Hyostrongylus* and *Cervicaprastrongylus*, the “0” papillae are cylindrical with parallel sides and are bluntly rounded distally, and Rays 8 are elongate, narrow, and relatively straight; consistently, Rays 9/10 $\geq 75\%$ of the length of Rays 8 (Durette-Desset and Chabaud, 1974; Gibbons and Khalil, 1982a, 1982b; Trach, 1986; Hoberg et al., 1993b). *Hamulonema* is further separated from *Hyostrongylus* by the structure of the spicules, with a prominent ostertagiine window and presence of a hooklike dorsal process in *H. hamata* and *H. kenyensis* (see Trach, 1986). We propose *Hamulonema* as a previously unrecognized genus that is morphologically consistent with placement among the Ostertagiinae.

Ostertagiine polymorphism and morphology

Polymorphism among males of single species among certain genera of the ostertagiines is now well established and recognized (reviewed in Drózdź, 1995). Polymorphism is typically manifested by the presence of morphologically distinct males that have often been placed in different genera, and consequently this has represented a major source of confusion for ostertagiine taxonomy (Lichtenfels and Hoberg, 1993; Drózdź, 1995; Hoberg et al., 2001). Usually, a single species is represented by a “major” morphotype, which is dominant, but co-occurs with a “minor” morphotype; both forms are present at fairly predictable frequencies within a host individual or host population (Drózdź, 1995). Essentially this represents a balanced polymorphism, although the drivers for this phenomenon remain undetermined.

Morphologically distinct, but conspecific, males are known for species in *Marshallagia*, *Orloffia*, *Ostertagia*, *Spiculopteragia*, and *Teladorsagia* (Drózdź, 1995). In contrast, polymorphism is currently unknown or does not occur among males of *Africanastrongylus*, *Cameloststrongylus*, *Cervicaprastrongylus*, *Hamulonema*, *Hyostrongylus*, *Longiststrongylus*, *Mazamastrongylus*, *Pseudommarshallagia*, and *Sarwaria* (Gibbons, 1977; Gibbons and Khalil, 1980; Lichtenfels et al., 1993, 1996; Hoberg et al., 2008). This distribution of polymorphism within the ostertagiines, and occurrence among males with either a 2-1-2 or 2-2-1 bursal formula, suggests that the phenomenon may have been associated with a common ancestor for these lineages.

Among polymorphic species, major morphotypes are usually characterized by relatively narrow and elongate spicules that trifurcate in the distal quarter, near 75–80% from the anterior. The accessory bursal membrane is membranous and contains narrow and filamentous “7” papillae. In contrast, minor morphotypes possess robust spicules that have a trifurcation near 60% and a genital cone that has a hypertrophied and cuticularized accessory bursal membrane, often termed a Sjöberg’s organ, perhaps best exemplified in species of *Teladorsagia*, and *Ostertagia* (e.g., Drózdź, 1965, 1995; Hoberg et al., 1993a, 1999).

Among the 23 other species of ostertagiines in the African fauna, specimens of *H. hamata* have not been found in association with a putative major morphotype (Mönnig, 1932; Ortlepp, 1961; Verster et al., 1975; Horak et al., 1982), whereas *H. kenyensis* has not been reported since the original description (Gibbons and Khalil, 1980). Based on currently recognized diversity for African ostertagiines, there are no species characterized with a 2-2-1 bursal formula (among *Africanastrongylus*, *Hyostrongylus*, *Cervicaprastrongylus*, or *Teladorsagia*) that could represent corresponding major morphotypes for either *H. hamata* or *H. kenyensis* (Hoberg et al., 2008). Species referred to *Longiststrongylus*, *Marshallagia*, *Ostertagia*, and *Pseudommarshallagia* are incompatible based on the structure of the 2-1-2 bursa, as previously outlined (Hoberg et al., 2008).

Interestingly, this suggests that *Hamulonema* contains 2 monomorphic species with attributes typical of minor morphotypes. Such a pattern has not been demonstrated previously among other ostertagiines where only single males are represented. Although the spicules of *Cervicaprastrongylus* are relatively robust, the accessory bursal membrane remains mem-

branous and is not strongly cuticularized; the accessory bursal membrane is also membranous among species of *Africanastromstrongylus*, *Camelostromstrongylus*, *Sarwaria*, and *Mazamastrongylus*. However, narrow spicules in species of *Longistromstrongylus* are also accompanied by a reduced and cuticularized accessory bursal membrane (E. P. Hoberg and A. Abrams, unpubl. obs.). Neither *Hyostrongylus* nor *Pseudomarsshallagia* are clearly accommodated within this framework (Graber and Delavenay, 1978; Trach, 1986).

African ostertagiine fauna revisited

Among 14 genera of the Ostertagiinae in the global fauna, 4 are entirely limited in distribution to Africa, including *Africanastromstrongylus*, *Hamulonema*, *Longistromstrongylus*, and *Pseudomarsshallagia*. Diversity for the subfamily was reviewed by Hoberg et al. (2008), who suggested that a disproportionate number of endemic genera occurred among African ungulates. These African genera may represent morphologically divergent and discrete or historically isolated lineages reflecting a pattern of geographic and host colonization since the Miocene (Hoberg et al., 2008). Among these endemic ostertagiines, only *Longistromstrongylus curvispiculum* (Gibbons, 1973) has been translocated with artiodactyl hosts from Africa as a component of introduced and exotic faunas in the United States and the United Kingdom (Gibbons and Khalil, 1977; Craig, 1993; Hoberg et al., 2001). Phylogenetic studies now in progress will serve to explore the dynamics and relationships of this complex mosaic which reflects episodic processes as drivers for diversification across relatively deep to shallow temporal scales (Hoberg and Brooks, 2008).

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